

Phylogenetic relationships within the genus *Cynanthus* (Aves: Trochilidae), with emphasis on *C. doubledayi*

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Abstract

We investigated the phylogeny of the genus *Cynanthus* and the taxonomic status of *C. doubledayi* using partial sequences of the mitochondrial DNA gene ND2 and three phylogenetic approaches: maximum parsimony, maximum likelihood, and Bayesian inference. Our results corroborate the monophyly of the genus and provide preliminary support for the validity of *C. doubledayi* as a full species (not a subspecies of *C. latirostris*, as traditionally considered). As an endemic of the coastal plain of southwestern Mexico, *C. doubledayi* corroborates the importance of this region for *in situ* speciation of birds and other taxa.

Key words: *Cynanthus doubledayi*, Species limits, Phylogeny, ND2 gene, Southwestern Mexico

Introduction

The hummingbird genus *Cynanthus* is currently composed of two species, the Broad-billed Hummingbird *C. latirostris* and the Dusky Hummingbird *C. sordidus* (AOU 1998), that are endemic to Mexico and the extreme southwestern United States (Fig. 1). Although the congeneric relationship of these two species has seldom been questioned, regardless of the genus to which they were assigned (e.g. Ridgway 1911), Navarro & Peterson (1999), based in morphological differences, suggested that two additional taxa deserve to be elevated to full species: *C. doubledayi* and the Tres Marias Islands Hummingbird *C. lawrencei*, rather than being included as subspecies of the Broad-billed Hummingbird, along with *C. l. latirostris*, *C. l. magicus*, *C. l. toroi*, and *C. l. propinquus* (Peters 1945; Friedmann *et al.* 1950; Schuchmann 1999; Dickinson 2003).

Cynanthus l. doubledayi is endemic to the coastal plain of southwestern Mexico from western Guerrero, Oaxaca, and, probably, to the western part of Chiapas (Howell & Webb 1995; Navarro & Peterson 1999; Schuchmann 1999; Dickinson 2003). *C. l. doubledayi* is similar overall to nominate *C. l. latirostris* but the forehead of the male is iridescent turquoise blue, the throat is deeper violet-blue, the under parts are generally more blue and the under tail coverts are black (Montes de Oca 1875; Ridgway 1911; Berlioz 1937; Moore 1939; Howell & Webb 1995; Navarro & Peterson 1999; Schuchmann 1999). The taxon was originally described by Bourcier in 1847 as *Trochilus doubledayi* with an erroneous type locality of Chiantla, Puebla. Cory (1918) corrected the type locality to Guerrero, after which Navarro and Peterson (1999) restricted it to Acapulco. Following its description, subsequent authors assigned *doubledayi* to various genera such as *Iache*, *Circe*, or *Hylocharis* (Ridgway 1911). *Iache nitida* Salvin and Godman (1899, type locality Chinautla, Puebla,

Mexico) is now considered to be a synonym of *doubledayi* (Friedmann *et al.* 1950; Howell & Webb 1995; Navarro & Peterson 1999).

It was Ridgway (1911) who first placed *doubledayi* in the genus *Cynanthus* and later authors included it as a subspecies of *C. latirostris* (Peters 1945; Friedmann *et al.* 1950; Schuchmann 1999; Dickinson 2003). Although Howell & Webb (1995) and Navarro & Peterson (1999) suggested that *C. doubledayi* is a separate species, this treatment was not adopted by the American Ornithologists Union checklist committee (AOU 1998 and subsequent updates available in the web site of the AOU: www.aou.org/checklist/index.php3), who considered it as one of two groups of *C. latirostris*. As in many groups of birds, the systematics of these hummingbirds was based on morphological characters such as coloration and tail cleft (Peters 1945; Friedmann *et al.* 1950; Navarro & Peterson 1999) in the absence of further information from other sources such as ecology, behavior, or genetics.



FIGURE 1. General distribution of the species of the genus *Cynanthus*. Squares indicate localities of samples collected for this study. Black = *C. doubledayi*, light gray = *C. sordidus*, dark gray = *C. latirostris*, arrow (Islas Marías) = *C. lawrencei*.

Here we address the phylogenetic relationships of the genus *Cynanthus* with special emphasis on clarifying the taxonomic status of the genus and of *C. l. doubledayi*, based on partial sequences of the ND-2 mitochondrial gene. We only studied samples of five of the subspecies of *C. latirostris*, because samples of *C. l. lawrencei* were not available. Although we had tissue samples for only seven individuals of *C. l. doubledayi*, but as far as we know these are the only samples available in scientific collections (we did not try to extract DNA from samples of the few older specimens available in collections).

Methods

Specimens of *Cynanthus* were collected throughout its range in Mexico except for the population of the Marías Islands (Fig. 1, Appendix 1). Tissues were stored in liquid nitrogen and voucher specimens (study skins and skeletons) were deposited at the Museo de Zoología “Alfonso L. Herrera”, Universidad Nacional Autónoma de México (MZFC). In addition we obtained tissues samples from the Smithsonian Tropical Research Institute (STRI) and Field Museum (FMNH) (see Appendix 1). The seven specimens of *C. l. doubledayi* were obtained after considerable effort distributed over several years, which could mean either that these hummingbirds are particularly difficult to collect or that their populations are small. Without knowledge about population size of *C. l. doubledayi* it is difficult to assess the percentage of the total haplotypes present in our small sample and, therefore, our results with respect to the status of *C. l. doubledayi* must be considered as preliminary.

DNA was extracted from each specimen using the Chelex 5% technique (Walsh *et al.* 1991) and the Qiagen Extraction Kit. Polymerase chain reaction (PCR) was carried out using a GeneAmp 9700 thermocycler following standard protocols. Primers L5215 and H5578 (Hackett 1996) were used to amplify the first fragment (351 bp) of gene ND2. PCR products were purified with a Gene Clean III kit (Bio 101) and a Millipore purification kit following standard protocols. A Perkin-Elmer ABI 373 sequencer was used to obtain the sequences. We sequenced in both directions and for several individuals. The ND2 sequences were congruent among themselves and with other sequences of hummingbirds in the Genbank. We translated the sequences to aminoacids to check for internal stop codons. The sequences were aligned by eye using Chromas 1.45 (32-bit) and they were corrected with the program Clustal X 1.81 (Thompson *et al.* 1999).

We used 42 individuals, of which 38 correspond to the ingroup and four to outgroup species. We used *Cyanophiaia bicolor* and *Hylocharis leucotis* because they are considered the closest relatives of *Cynanthus* (AOU 1998; Schuchmann 1999; Dickinson 2003); we used the more distantly related *Amazilia beryllina* and *Phaethornis mexicanus* (AOU 1998) to test the monophyly of the genus.

We performed phylogenetic analyses using three approaches: Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) using the 21 unique haplotypes obtained: seventeen correspond to the genus *Cynanthus* and four to the outgroup. These partial sequences were deposited on Genbank with the accession numbers reported in the Appendix. MP analyses were conducted in PAUP 4.0b (Swofford 2001) with a heuristic search using a TBR branch-swapping option and with all positions equally weighted. Support for each node was obtained by 1000 bootstrap replicates (Felsenstein 1985). For ML and BI analyses we used ModelTest 3.6 (Posada & Crandall 1998) to determine the model of evolution that best explained our data. ML was conducted in PAUP 4.0b (Swofford 2001) using heuristic search and nodal support was estimated via 100 bootstrap replicates. BI analyses were conducted using MrBayes 2.0 (Huelsenbeck & Ronquist, 2001). We ran four independent analyses. Each analysis consisted of four chains, random starting trees, and uniform prior distribution of parameters. The chains were run for ten million generations, sampling trees every 250 generations. The asymptote was determined visually, burn-in trees discarded, and the remaining trees used to estimate Bayesian posterior probabilities. We considered that clades were strongly supported if they were present in =95% of the sampled trees (Huelsenbeck & Ronquist 2001; Wilcox *et al.* 2002).

Results

Of the 351 bp of ND2 sequenced, 211 were conserved sites and 140 were variable; 76 variable sites were parsimony informative. The nucleotide composition is as follows: C = 31.5%, A= 30.7%, T=24.7% and G= 13.1%. The model of molecular evolution that best fitted our data was TrN+I (Nst = 6, rates = equal, freqA= 0.2900, freqC =0.098, freqG= 0.1447, freqT= 0.2554).

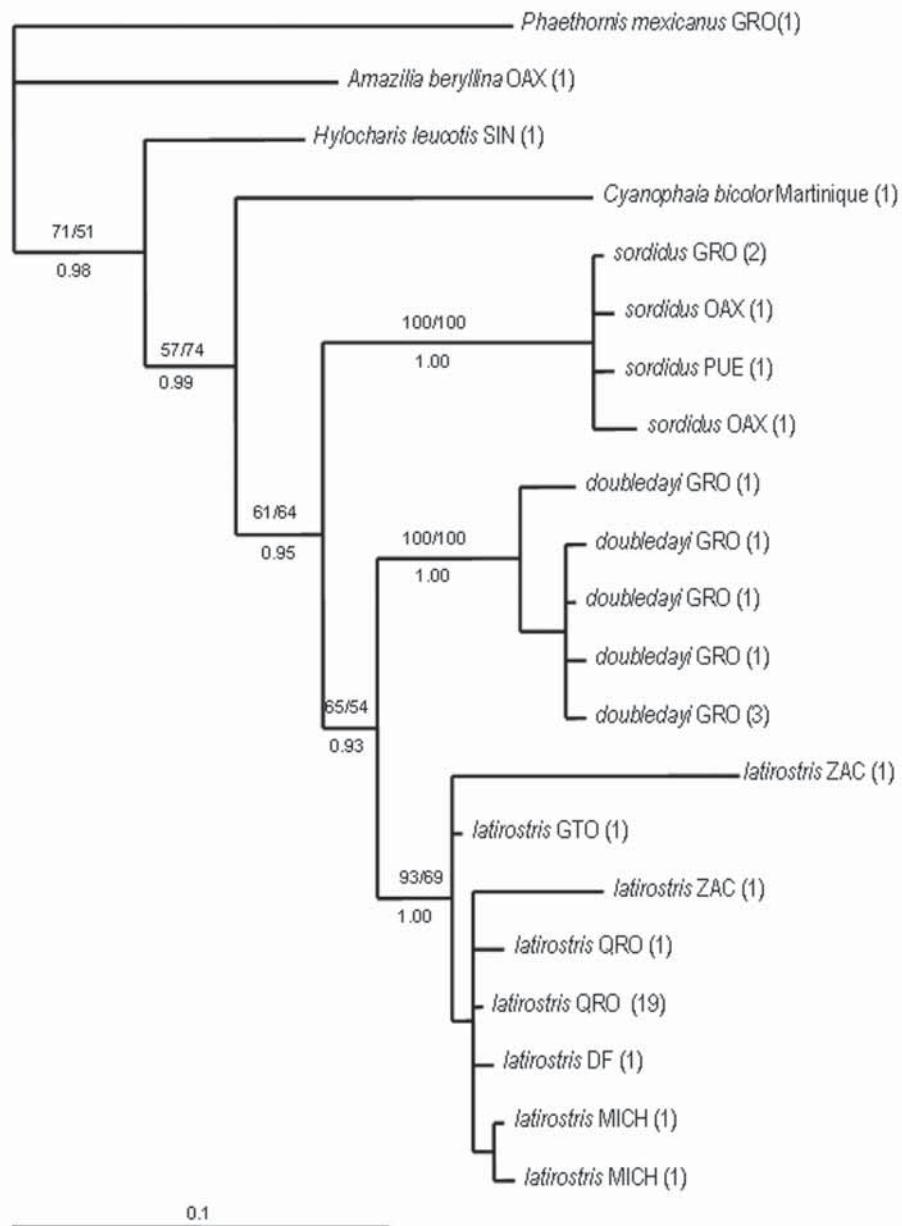


FIGURE 2. Bayesian tree using partial mtDNA gene ND2 using the model described in the text. Branching patterns of ML and MP analyses agree with the one depicted. Values above the node correspond to parsimony and maximum likelihood bootstraps, below the node correspond to posterior probabilities. Numbers in parentheses correspond to the number of shared haplotypes. Abbreviations refer to Mexican states: GRO = Guerrero, OAX = Oaxaca, SIN = Sinaloa, PUE = Puebla, ZAC = Zacatecas, GTO = Guanajuato, QRO = Querétaro, DF = Distrito Federal, MICH = Michoacán.

The MP analysis with 1000 bootstrap replicates found 36 most parsimonious trees, from which we constructed a strict consensus tree ($L = 234$, $CI = 0.778$, $HI = 0.222$). The 36 most parsimonious trees were variants of the same theme and in no case did the major groupings (“species”) break up or mix up. The consensus tree had the same topology as the one obtained in ML and BI analyses (Fig. 2). In this topology, the monophyly of *Cynanthus* is clear (MP: 61; ML: 64; BI: 0.95 pp) and *Cyanophaia bicolor* appears as its sister taxon (MP: 57; ML: 74; BI: 0.99 pp). Within *Cynanthus* we found three main clades: 1) *C. sordidus* (MP: 100; ML: 100; BI: 1.00 pp), 2) *C. latirostris* (MP: 93; ML: 69; BI: 1.00 pp) and 3) *C. doubledayi* (MP: 100; ML: 100; BI: 1.00 pp). In all three analyses (MP, ML and BI) *C. doubledayi* was the sister taxon of *C. latirostris*. Furthermore,

all three methods reveal strong support values (MP: 100, ML: 100, BI: 1.0 pp) for the monophyly of *C. doubledayi*.

Despite using a small number of base pairs (351) obtained from a single mitochondrial gene (ND2), the clear picture obtained led us to consider that our sample was sufficient to meet the objective of addressing the monophyly of the genus *Cynanthus*. With respect to our second objective of clarifying the taxonomic status of *C. l. doubledayi*, although our main results (see previous paragraph) show a simple and clear picture, the small sample size (see methods) make us consider our results as preliminary.

Discussion

The fact that over 50% of hummingbird genera are monotypic gives an indication of how problematic is the systematics of this fascinating group of birds (AOU 1998). Morphological, behavioral and physiological convergence due to their specialized ecological niche is partially responsible for this situation (Bleiweiss 1998). For this reason, the use of DNA sequences seems particularly appropriate for the clarification of relations between genera and for the definition of species limits. The three phylogenetic approaches used in this study (Maximum Parsimony, Maximum Likelihood and Bayesian Inference) produced results that clearly support the monophyly of *Cynanthus* and identify *Cyanophiaia* as its sister taxa.

The high posterior probabilities for monophyly of *C. doubledayi* are consistent with its recognition as a species separate from *C. latirostris* based on morphology (Ridgway 1911; Howell & Webb 1995; Navarro & Peterson 1999, 2004). One of the characters used by those authors to separate this species was the unique combination of the color of the breast and under parts, which are bluer than in *C. latirostris*, and our data support this as diagnostic for *C. doubledayi*. In addition there are slight differences found in vocalizations and the allopatric summer distributions of both forms (personal observations). During the winter, both forms are possibly parapatric at the Balsas Basin, as suggested by Howell & Webb (1995). Although it is clear that the mtDNA differences alone are not enough to define a species, these results, together with previously known differences in other traits (de Queiroz 1998; Helbig *et al.* 2002; Omland *et al.* 2006) such as plumage, vocalizations and distribution, support the specific status of Doubleday's Hummingbird.

C. doubledayi has a restricted distribution that includes the dry forests of the lowlands and submontane slopes (Navarro 1992) along the Pacific coast of the states of Guerrero and Chiapas in Mexico. Pacific dry forests are structurally and ecologically very heterogeneous (Murphy & Lugo 1986) and have a complex history associated with the formation of major mountain ranges and paleoclimatic events that have isolated large areas of these forests (Becerra 2005). These factors probably promoted the diversification of the associated faunas. Further comparative studies are needed to assess the role and timing of these climatic changes in the diversification of the pacific lowlands avifaunas. However, the available evidence gives a clear indication of the importance of western Mexico as a major area of bird speciation (Peterson & Navarro 2000, García-Trejo & Navarro 2004).

Acknowledgments

We thank S. López, L. A. Sánchez, B. Granados, V. Rodríguez, H. Vázquez-Miranda, and Y. Nakazawa for field assistance, and L. Márquez and A. Gordillo for technical support. We also thank J. Bates (FMNH) and E. Bermingham (STRI) for supplying us with some samples. The manuscript was improved by comments of C. Cordero, L. León-Paniagua, R. Faucett, K. E. Omland, A. T. Peterson, and two anonymous reviewers. This research was funded by PAPIIT-UNAM (IN 208700, IN211407-2 and IN 233002), SEMARNAT-CONACyT Sectorial Fund (C01-0265), CONACyT (R-27961) and DFG (GA 788/1 to JGM). GMGD was supported by PROBETEL-UNAM and the Small Grants Program of the Hummingbird Society.

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Appendix 1. List of haplotypes, localities, vouchers/sample IDs and GenBank Accession numbers

Hap- lotyp- e	Species	Subspecies	Catalogue No./Museum ^a	Locality	GeneBank Accession Number
1	<i>C. latirostris</i>	<i>magicus</i>	CONACYT 395MZFC	Zacatecas, Rancho Chalchisco, 6 Km SW Jalpa	EU418745
2	<i>C. latirostris</i>	<i>magicus</i>	CONACYT 387MZFC	Zacatecas, Rancho Chalchisco, 10 Km W Jalpa	EU418744
3	<i>C. latirostris</i>	<i>magicus</i>	CONACYT 368MZFC	Zacatecas, Rancho Chalchisco, 6 Km SW Jalpa	EU418742
	<i>C. latirostris</i>	<i>magicus</i>	CONACYT 427MZFC	Zacatecas, Rancho Chalchisco, 6 Km SW Jalpa	EU418742
	<i>C. latirostris</i>	<i>magicus</i>	CONACYT 428MZFC	Zacatecas, Rancho Chalchisco, 6 Km SW Jalpa	EU418742
	<i>C. latirostris</i>	<i>toroi</i>	CONACYT 875MZFC	Michoacán, Colola, Las Haciendas	EU418742
	<i>C. latirostris</i>	<i>propinquus</i>	CONACYT 1565MZFC	Guanajuato, Tinajas de Pastores, Yuriria	EU418742
	<i>C. latirostris</i>	<i>magicus</i>	CONACYT 1567MZFC	Jalisco, El Chante, Autlán	EU418742
	<i>C. latirostris</i>	<i>magicus</i>	CONACYT 1568MZFC	Jalisco, El Chante, Autlán	EU418742
	<i>C. latirostris</i>	<i>latirostris</i>	QRO 012MZFC	Querétaro, San Miguel Palma	EU418742
	<i>C. latirostris</i>	<i>latirostris</i>	QRO 053MZFC	Querétaro, Presa Zimapán, 4 km NW Tziquia	EU418742
	<i>C. latirostris</i>	<i>latirostris</i>	QRO 204MZFC	Querétaro, Rancho 99	EU418742
	<i>C. latirostris</i>	<i>latirostris</i>	QRO 246MZFC	Querétaro, La Florida	EU418742
	<i>C. latirostris</i>	<i>latirostris</i>	QRO 421MZFC	Querétaro, Higuerillas, 5 Km antes de Higuerillas	EU418742
	<i>C. latirostris</i>	<i>toroi</i>	CONACYT 1061MZFC	Michoacán, Presa Infiernillo, 1.5 Km N Campamento CFE	EU418742
	<i>C. latirostris</i>	<i>toroi</i>	CONACYT 1062MZFC	Michoacán, Presa Infiernillo, 1.5 Km N Campamento CFE	EU418742
	<i>C. latirostris</i>	<i>toroi</i>	CONACYT 1092MZFC	Michoacán, Presa Infiernillo, 1.5 Km N Campamento CFE	EU418742
	<i>C. latirostris</i>	<i>toroi</i>	CONACYT 1093MZFC	Michoacán, Presa Infiernillo, 1.5 Km N Campamento CFE	EU418742
	<i>C. latirostris</i>	<i>toroi</i>	CONACYT 1099MZFC	Michoacán, Presa Infiernillo, 1.5 Km N Campamento CFE	EU418742
	<i>C. latirostris</i>	<i>toroi</i>	CONACYT 1102MZFC	Michoacán, Presa Infiernillo, 1.5 Km N Campamento CFE	EU418742
	<i>C. latirostris</i>	<i>latirostris</i>	HGO-SLP 077MZFC	San Luis Potosí, El Mezquital	EU418742
4	<i>C. latirostris</i>	<i>latirostris</i>	394365FMNH	Querétaro, 2 Km S Estación Bernal	EU418741
5	<i>C. latirostris</i>	<i>latirostris</i>	CONACYT 1025MZFC	DF, Coyoacán, Facultad de Ciencias	EU418743
6	<i>C. latirostris</i>	<i>propinquus</i>	CONACYT 1566MZFC	Guanajuato, Tinajas de Pastores, Yuriria	EU418746
7	<i>C. latirostris</i>	<i>latirostris?</i>	CONACYT 851MZFC	Colima, Tepames, Las Cuevas	EU418757
8	<i>C. latirostris</i>	<i>latirostris?</i>	CONACYT 861MZFC	Colima, Tepames, Las Cuevas	EU418758
9	<i>C. doubledayi</i>		CONACYT 896MZFC	Guerrero, Tecpan, Fracc. Laguna Nuxco	EU418749
	<i>C. doubledayi</i>		CONACYT 933MZFC	Guerrero, Tecpan, Fracc. Laguna Nuxco	EU418749
	<i>C. doubledayi</i>		CONACYT 936MZFC	Guerrero, Tecpan, Fracc. Laguna Nuxco	EU418749
10			CONACYT 902MZFC	Guerrero, Tecpan, Fracc. Laguna Nuxco	EU418747
11			CONACYT 904MZFC	Guerrero, Tecpan, Fracc. Laguna Nuxco	EU418748
12			CONACYT 988MZFC	Guerrero, San Luis Acatlán, 2 Km NE de El Carmen	EU418750
13			CONACYT 991MZFC	Guerrero, San Luis Acatlán, 2 Km NE de El Carmen	EU418751
14			OMVP 733MZFC	Oaxaca, Yucunino, Cerro Piedra Larga	EU418754
15			OMVP 747MZFC	Oaxaca, Cerro Piedra Larga	EU418755
16			PUE 57MZFC	Puebla, Venta Salada, 8 Km S Coxcatlán	EU418752

17	<i>C. sordidus</i>	UAG 13MZFC	Guerrero, Iguala, Mexcaltepec	EU418753
	<i>C. sordidus</i>	OMVP 872 MZFC	Oaxaca, Distrito de Teotitlan, 3 km SE Santiago Quiotepec	EU418753
18	<i>H. leucotis</i>	SIN 020MZFC	Sinaloa, El Batel	EU418759
19	<i>P. mexicanus</i>	BMM 38MZFC	Guerrero, El Iris	EU418760
20	<i>A. beryllina</i>	BMM 265MZFC	Oaxaca, Sierra de Miahuatlán, Río Salado	EU418761
21	<i>C. bicolor</i>	MA-CB5STRI	Martinique, Fond Baron	EU418756

^aMuseum keys MZFC = Museo de Zoología “Alfonso L. Herrera”, Facultad de Ciencias, UNAM; FMNH = Field Museum of Natural History, STRI = Smithsonian Tropical Research Institute, Panamá.